HABITS OF THE CRIMSON-CRESTED WOODPECKER IN PANAMA

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I studied the Crimson-crested Woodpeckers (*Campephilus* [*Phloeoceastes*] *melanoleucos*) in the Panama Canal Zone in February 1965 and from November 1970 to February 1971, a period which included the end of the rainy season when nesting began and the onset of the dry season when young were fledged. The behavior of this species resembles that described by Tanner (1942) for the Ivory-billed Woodpecker (*Campephilus principalis*) and has not hitherto been the subject of any detailed reports, with exception of notes by Short (1970*b*), as far as I am aware. In Short's opinion (1970*a*), *Phloeoceastes* should be merged in *Campephilus* and I have adopted this terminology.

While the aim of present studies was to learn as much as possible about the total behavior of *C. melanoleucos*, the problems raised by its similarity in size and coloration to the sympatric Lineated Woodpecker (*Dryocopus lineatus*) were kept in mind, thanks to the ideas of Cody (1969) on why this parallelism exists. Actual field observations, however, failed to support his interesting theories, which are dealt with in greater length in a final discussion.

STUDY AREAS

I studied Crimson-crested Woodpeckers in five localities of which three, Madden Forest Reserve, Limbo Hunt Club, and Barro Colorado Island (BCI), were, for the most part, mature forests. Of the other two areas, one was of second growth forest 10 to 20 m in height at Cardenas Village where I lived and the other at Frijoles, an area under partial cultivation opposite Barro Colorado Island. The Crimson-crested and Lineated Woodpeckers were sympatric in all five of these localities, as indeed they are in much of South America.

METHODS OF COMMUNICATION

Instrumental Expressions

Drumming.—Drumming is typically a strong blow followed by short, weak, vibratory roll, "DA-drrr." Such bursts usually come at a rate of one to two per minute, three per minute being a fast rate. This drumming serves a number of functions. Single "DA-drrs," given occasionally throughout the day, enable members of a pair to keep in touch as they travel through woods together; duets of them continuing for periods of up to 20 minutes may occur at the height of courtship and just prior to copulation; while louder drumming, delivered against a resonating stub, is usually related to territorial disputes and assertions of dominance. This abbreviated drumming of *C. melanoleucos*,

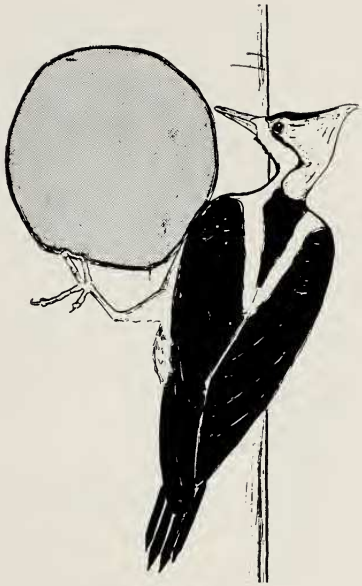

FIG. 1. Female Crimson-crested Woodpecker drum-taps at rim of recently completed nest hole as mate approaches.

which at times can be no more than a single "DA," appears to be the same as that described by Tanner (1942) for the Ivory-billed and by Short (1970*a* and *b*) for the Magellanic (*C. magellanicus*) and other *Campephilus* woodpeckers in South America. Although both sexes of *C. melanoleucos* drum, males drum far more than females during the nesting season.

Pileated Woodpeckers (*D. pileatus*) (Kilham, 1959) strike a sharp rap with their bills against any surface they happen to be on when nervous or excited. According to Bock (1963), the genus *Campephilus* is an offshoot, phylogenetically, of *Dryocopus* and one might wonder whether the single drumming of *Campephilus* is not derived from the rapping of the latter genus. An observation of Tanner (1942) on the Ivory-billed Woodpecker is of interest here, for he noted that "The adults always were disturbed and excited whenever I first found a nest." In addition to giving calls they "often double-rapped or pounded on stubs or limbs of the nest tree and nearby trees." Thus, the drumming was done in the same context as the rapping would be done for *D. pileatus*.

Drum-tapping.—As discussed in a preceding report (Kilham, 1959), most woodpeckers tap at a regular and countable rate at the time of excavation of a nest hole. Pileated Woodpeckers, on the other hand, have a more rapid

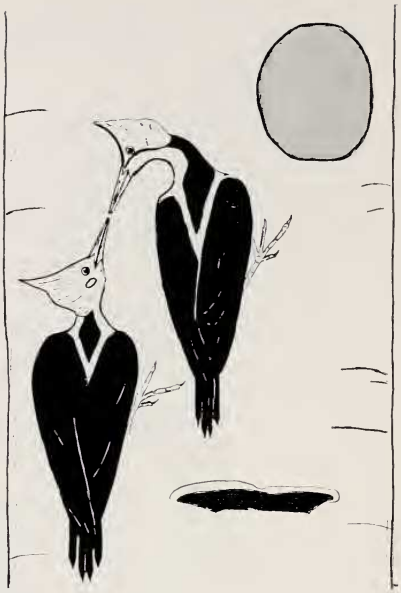

FIG. 2. Female Crimson-crested Woodpecker backs down from nest hole to touch bills with her mate who reaches up toward her.

roll taking the place of tapping, which I have called "drum-tapping." Crimson-crested Woodpeckers drum-tap in the same manner as Lineated and Pileated Woodpeckers, both at the rim of the nest hole at time of excavation (Fig. 1), but also down inside the nest at time of relief at the nest, a habit also described by Sielmann (1958) for the European Black Woodpecker (*D. martius*).

Wing noises.—Crimson-crested Woodpeckers can fly silently. They often, however, make a heavy sound, even in flying short distances, that doubtless keeps each member of a pair informed when the other moves and in what direction. Heavy wing noises are a feature of conflicts.

Displays

Bill-touching.—At times of most active courtship, the woodpeckers of a pair may come close to one another, crests raised and even curled forward, then fence gently, making contact for roughly half the length of their bills. This interest in bills at time of courtship may be related to the way a male pecks down at the bill of the female while copulating. Ivory-billed Woodpeckers touch bills in courtship according to Tanner (1942) and Allen and Kellogg (1937) wrote that as a female climbed up a pine toward her mate "he bent his head downward and clasped bills with her." Although I noted a

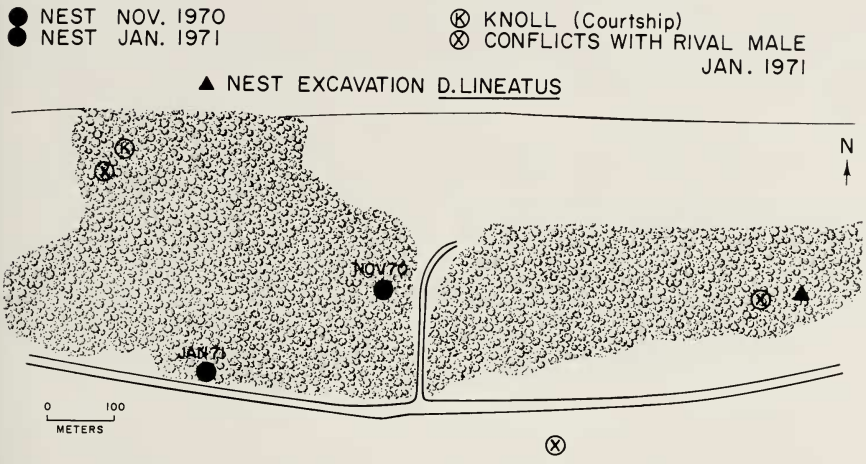

Fig. 3. Territory of Pair A of Crimson-crested Woodpeckers at Cardenas Village.

similar bending down on several occasions, as illustrated in Figure 2. I never observed bill clasping with *C. melanoleucos*.

Vocalizations

Alarm notes.—Notes of moderate disturbance made, for example, when one comes too close to a nest excavation are *ca* and *ca-wa-rr-r* often repeated. A sharp, high-pitched *ca* given alone was the only vocalization heard in several conflicts between males. Shrill, piping *put put puttas* given by both males and females are expressive of high excitement. These may be kept up for minutes on end. On the whole, however, Crimson-crested Woodpeckers are relatively silent birds, giving way to alarm notes with far less frequency than the related Lineated Woodpeckers.

Intimate notes.—These low notes are expressive of closeness of pair bonds, being given just prior to coition and at times when one partner relieves the other at excavating. Variations include *wuk wuk*, *wrr wrr*, *wun wun*, and *uh uh* among others.

Main breeding call.—A tree-frog-like *kwirr kwirr-ah* or *squeer squeer-ah-hah*.

Comparisons to other species.—Short (1970*b*) records a three-noted call *wink-at-chew* for *C. melanoleucos* in Argentina. Vocalizations of *C. magellanicus* (Short, 1970*b*) are given in more detail and here the double-noted calls, *wieeer* and *kee-argh* (harsher, more drawn out) appear somewhat similar to the *kwirr-ah* and *ca-wa-rr-r* notes described above for *C. melanoleucos*.

COURTSHIP AND COPULATION

The following activities of Crimson-crested Woodpeckers, as well as the excavation of nest holes, with exception of Pair E, took place in the rainy season.

Pair A.—The woodpeckers of Pair A frequently came to a knoll (Fig. 3) at the edge of woods by Cardenas Village for early morning courtship and preening, the male (MA) always to a special place on his tree and the female (FA) to hers. These trees were about 14 m tall and 10 m apart. Here the two began a duet of drumming at 06:10 on 22 November 1970. After 15 minutes of low bursts, one or two per minute from each, MA flew to FA's tree and I heard low notes then as well as five minutes later when FA moved out onto a horizontal limb. Here she crouched low in a crosswise position as MA approached. He mounted in full coition, pecking gently down at her bill four or five times as he gradually fell to the left in establishing cloacal contact.

This copulation suggested that the pair must have a nest nearing completion and on 26 November I was led to it at 16:00 by the sound of FA excavating. She took alarm and flew out, then drummed on nearby trees as if disturbed. I returned again in the late afternoon. The woodpeckers were feeding in trees close-by when, at 17:20, FA flew to the hole and clung to its lower rim. When MA alighted a meter below, she drum-tapped on the rim of the hole (Fig. 1) and as he hitched upward, she moved down to meet him, bending over to fence bills (Fig. 2) as he stretched upward. All now looked well for actual nesting. The way a pair of Collared Araçaris (*Pteroglossus torquatus*) dispossessed the woodpeckers of their completed hole 20 minutes later is described beyond.

Five days later, on 2 December, the two Woodpeckers, now without a nest, had returned to the knoll (Fig. 3). MA drummed at an uneven rate of 11 times in 10 minutes at 06:23, but FA, on her tree, did not respond. When he flew to her, however, the two fenced lightly with their bills. FA moved on a less horizontal part of the trunk and crouched low, but MA, taking no apparent interest in this invitation to coition, flew away. On the following morning MA drummed again, with only one burst in reply from FA. The two preened in leisurely fashion for 35 minutes, then left. It thus appeared on succeeding days that, with loss of their nest, the woodpeckers gradually lost interest in courtship.

I now felt there would be little to observe further with this pair when on 15 December I heard *kwirr-kwirra* notes by the knoll when MA alighted on the trunk of a slender tree, to be joined almost immediately by FA, both being at the same level as they bent heads together to touch bills. The crests of the two were raised to the full and curled forward. They returned to their original positions, only to bend heads together on the other side of the trunk to fence again. Both now flew to the knoll and drummed a brief duet before a longer period of leisurely preening. Had the woodpeckers found a new nesting site as the renewal of courtship activities suggested? I had no further indication of this until 1 January when at the comparatively late hour of 18:45 I saw the pair on a bare tree near the knoll in full copulation. From here, after feeding for five minutes, they flew east. With this direction as a clue I was able to find their nest, in which they were to hatch young, a few days later.

Pair B.—At 06:10 on 26 November drumming led me to find a male Crimson-crested Woodpecker on the limb of a dead tree above Madden Forest. A female Lineated Woodpecker alighted briefly on the same limb but after she had left, the female Crimson-crested, whom I could not see, drummed five or six times, then flew to her mate. I heard low notes, then witnessed full coition lasting possibly 10 seconds. Afterwards the two birds

preened in leisurely fashion for 10 minutes, then flew to feed in the forest. At 07:00 the female gave a single *kwirr-a*. After a pause, the male flew to her, there were more low notes, and a second copulation, not well seen, followed. This was 35 minutes after the first one.

EXCAVATION OF NEST HOLES

Trial nest stub.—Not all pairs of Crimson-crested Woodpeckers were able to find suitable nest stubs. Pair C, for example, had already tried to excavate one stub when, at 09:25 on 24 December, I found the male carving an entrance in a second one. His mate remained nearby making querulous *wer wer* and *wuk wuk* notes until she took over the excavating at 09:40. Her interest, however, waned after five minutes and she circled up the stub, pecking here and there as if to test the nature of the underlying wood, which was probably too hard to excavate, before flying away. She thus appeared more critical of the stub as a nesting site than her mate. Little further progress was ever made with entranceway and by early February Pair C had still failed to find a place to nest. From such observations I came to believe that suitable stubs in this and other parts of Barro Colorado Island, as well as other localities, were generally in short supply.

Successful nest stubs.—Both males and females excavated and their greetings at times of changing over were expressive of attachment to the nest hole as well as to each other. At 10:45 on 26 December, for example, the male at Nest D drum-tapped when inside the hole with head still visible, made low notes, then drum-tapped again when his mate flew over to take his place. She tossed some sawdust from the entrance but spent most of her time looking out. When Male D returned in 15 minutes, she immediately disappeared to drum-tap at the bottom of the cavity. He peered in at her several times before she squeezed out by him to fly away. MD then tossed out sawdust. As with FD, however, he was soon looking out idly and I believed from this and subsequent behavior that the nest was ready for egg laying.

The woodpeckers of Pair E were late in excavating in comparison with Pair D, for they did not begin until late in January. Their hesitancy to use the stub finally chosen was probably due to the mass of epiphytes at the top, together with the lianas that might have encouraged arboreal mammals or other unwanted neighbors. The pair had, however, carved an entrance by 22 January. The female did most of the excavating at this nest and change-overs, when they did occur, were much the same as for Pair D with one exception. This was on 31 January. Male E had been excavating when his mate flew to the hole making low notes. Instead of dropping out of sight to drum-tap, ME remained by the hole to meet his mate directly and the two touched bills a number of times before he flew away.

NESTING

Greeting ceremonies in the first few days of incubation were much the same as in the previous period in regard to drum-tapping, but changes soon became evident when the birds became silent, increasingly undemonstrative, and no longer looked out from entrances. When MD came to his nest hole at 16:00 on 8 January, his mate swung out of the hole in silence, the two woodpeckers resting side-by-side below the hole momentarily without other ceremonies before she flew away.

Times between change overs are long for *C. melanoleucos*. In waits of one and a half hours or more I never saw a woodpecker return after leaving. Skutch (1969), however, in waiting for extended periods at a nest of the closely related Pale-billed Woodpecker (*C. guatemalensis*), noted the female as spending four and a half hours on the eggs and her mate as remaining on them from 12:15 until dark without being relieved.

Nestling period.—The behavior of the woodpeckers at Nest D changed with the hatching of the eggs, their greater restlessness being exemplified by the following observations: On 15 January MD, after looking out from the hole for five minutes, flew out at 13:45 to preen for a few minutes on an adjacent tree, then re-entered to brood the nestlings. The longest time he spent away from the nest in the course of two and a half hours was 10 minutes.

On 22 January FD had been brooding for a half hour when she flew out, leaving the young unattended for 45 minutes before MD arrived and entered. FD returned almost immediately, replacing him within a few minutes. Her attention to the nest was closer than that of her mate on this and succeeding days, as she would generally stay near the nest when not in it, whereas MD might, at times, be away for more than three hours.

Other events of special interest at Nest D during the nestling period can be summarized as follows:

1) Neither parent ever brought visible prey to feed their young. It is conceivable, however, that they might have done so had the young survived longer, for Tanner (1942) describes Ivory-billed Woodpeckers as carrying large grubs to well-grown nestlings.

2) FD and MD were both together in the nest on two occasions. Thus, on 30 January MD entered while his mate was inside, only to leave a few minutes later and on the following day, under similar circumstances, he remained inside with her for five minutes.

3) MD became increasingly apprehensive as the nesting period progressed, delaying each entry by much looking about and bowing into the hole, only to withdraw. Whether the predator that finally destroyed the nest (if predation was the cause) was in the vicinity I did not know, but on nearly every visit

to Nest D I did see a pair of Spectacled Owls (*Pulsatrix perspicillata*) almost within sight of it.

I found Nest D devoid of activity when I came to it on 7 February. The entrance was undamaged and I could find no clue as to why the nest had failed. In looking about in woods nearby I was able to locate the parents and to follow them for one and a half hours. Their behavior was now much as in the pre-nesting season, with no sign that they any longer had young to feed.

Tanner (1942) speaks of three nests of Ivory-billed Woodpeckers from which the young disappeared mysteriously and the nest of the Pale-billed Woodpecker observed by Skutch (1969) also failed. He noted a large black snake in the vicinity. It would seem that snakes may be likely predators of such woodpeckers when entrances are undamaged.

YOUNG AFTER LEAVING NEST

I was watching a male Crimson-crested Woodpecker digging out grubs from a well-rotted stub on 22 January on Barro Colorado Island when a second woodpecker in adult female plumage alighted 25 cm away. She made no effort to feed herself but preened lightly, making *k-da k-da* begging notes much of the time. The male paid no seeming attention until, on encountering a huge larva (4 cm long and 1½ cm in breadth), he leaned over and fed it to her. Meanwhile, a second female, I believed the mate of the male, joined the other two. This second female, unlike the first one, dug out her own food. The two females got along peacefully although later on I had evidence of a brief conflict between them.

The male did not feed the begging female again in the course of the hour that I followed them. She foraged for herself occasionally but much of the time she followed him so closely that she was almost at the tip of his tail, whether he was feeding along the under or top side of a limb. It seemed possible that she was a young of the year before and while this may seem a long time for a young one to stay with parents, it does fit a situation described by Short (1970*b*) for *C. melanoleucos* in Argentina as well as by Tanner (1942) who wrote of *C. principalis* as follows:

> "The young birds usually leave or are driven away by the following nesting season, but the single male that was raised by the John's Bayou birds in 1938 stayed in that territory through the following spring. The female of the pair frequently tried to drive him away, but he would only dodge, sulk, and return. The old male paid little or no attention to his yearling son."

The first juvenile I encountered on Barro Colorado was on 31 January when continued *k-arr k-arr* disturbed notes attracted me to one at the edge of a gap in the forest. Its mother in the same clearing gave her *k-wirr k-wirr-a* notes, then flew off. The young one followed and later I found it close beside

her as she dug for grubs in a dead stub. The only other encounter with juveniles was on 19 February 1965 when, as described below, one adult female, attended by two juveniles, had a confict with a second female.

TERRITORIAL AND AGONISTIC BEHAVIOR

Female vs female.—Two females alighted low on a series of trees on the morning of 19 February 1965, shifting around trunks as one tried to strike the other, or made a display of doing so for over 15 minutes. The presence of several juveniles indicated that the conflict, possibly a territorial one, had come at the end of the nesting season.

Male vs male.—Sounds of much drumming had come from Territory E on the morning of 27 December. When I followed these into the woods at 13:00, I found two males, one pursuing the other in short, heavy-sounding flights from one to another of four trees centering on a tall stub, to which they often returned. The stub, although unsuitable in a number of aspects, was large enough for nesting. When the woodpeckers came to rest, I noted two types of more direct conflicts: In one that lasted five minutes, one male clung almost upside down below a large limb, while the other, perched on top, half-opened his wings each time the first one tried to come around from below. When the two flew, it was to continue with an even milder type of encounter on a tree trunk nearby. Here one backed down as the other retreated backward. Finally both flew in opposite directions with the territory owner going to a large dead limb where he drummed in slow but resounding fashion for six minutes. He then attacked the intruder again. All of the fighting was silent except for two sharp *ca* notes. The males were still engaged when I left 50 minutes later.

A somewhat different and even milder conflict between males took place on 12 January at Cardenas Village, where Female A was probably incubating eggs. MA was preening and occasionally drumming at "the knoll" (Fig. 3) on what was usually FA's drumming tree when, at 07:08, a second male arrived on MA's usual drum tree 10 m away. MA did not appear disturbed. He continued to preen and drum as before, giving about five bursts to every single one given by the intruder. The latter clung almost immobile the whole time. Possibly, being well within the territory of MA, he was intimidated. This was suggested when he suddenly flew toward MA, then changed his mind in mid-air, and returned to his original position. Five minutes later he again flew, but this time in an opposite direction.

The intruder again returned some minutes later to a tree close by MA. The conflict ended at the knoll when MA left soon afterward, followed in a minute or two by the second male. This was possibly the first of a series of encounters taking place on subsequent mornings between the two males.

The above encounters were all mild in nature. There were no accompanying vocalizations, no bill-wavings, or for the most part any threat displays, and no direct clashes such as one can observe among temperate zone species such as the Pileated Woodpecker (Kilham, 1959). It may be that tropical species, being under more pressure from predators, cannot afford to attract attention to themselves when engaged in conflicts. Short (1970*b*), however, gives a description of a more conspicuous conflict between two males of *C. robustus*.

INTERACTIONS WITH OTHER SPECIES

Collared Araçaris.—The mildness and seeming lack of aggressiveness of Crimson-crested Woodpeckers was exemplified, in a different context, when several Collared Araçaris took over the just completed nest hole of Pair A on 26 November. After drum-tapping and bill-touching by the hole, these woodpeckers had appeared comfortably on the way to nesting when MA entered the hole to roost for the night at 17:33. He was soon looking out, however, as if nervous. Seven minutes later he slipped out and moved around to the rear of the stub, being joined by his mate as a toucan flew to the hole and put its bill in several times. The woodpeckers made a few low *krr* notes but gave no sign of resistance. They simply flew off and as far as I know they never returned. A feature of this performance was that the toucans did not appear too confident. They did not roost in the hole on the 26th and when I returned to the nest stub at 17:25 four evenings later, I found them still chary about entering, for they rested nearby for 20 minutes as if looking the situation over before doing so. A few nights later, on the contrary, they arrived at dusk and entered directly. They had thus won the hole without any show of aggressiveness.

Reaction to a marmoset.—On 24 February 1965 I watched a male Crimson-crested Woodpecker feeding in a mass of vines at the top of a tall stub in company with two marmosets (*Oedepomidas geoffreyi*). A marmoset came down a vertical liana on which a woodpecker was working. Neither species paid any attention to the other, even though they passed within 5 to 7 cm of each other on either side of the vine. Crimson-crested Woodpeckers did, however, become much excited by monkeys on one occasion. This was when the members of Pair E were excavating a nest not far from a cage of *Cebus* monkeys on Barro Colorado on 26 January. Loud screaming from the cage upset both birds to the extent that they made almost continuous *put-put-putta* notes for 10 minutes.

On the whole, however, I found Crimson-crested Woodpeckers relatively unexcitable as compared with Lineated Woodpeckers. Their tameness in fact was of great aid in observing them. It would seem that Tanner (1942) had a similar experience in noting that Ivory-billed Woodpeckers became used

to people so rapidly that "in a day or so (they) would pay little or no attention to one a moderate distance away."

FEEDING BEHAVIOR

Methods of Foraging.—The feeding behavior of Crimson-crested Woodpeckers was separable into the following categories:

Pecking.—The uncovering of prey with relatively few blows against bark of superficial layers of wood.

Percussion.—While a woodpecker may deliver many blows per minute in pecking, not all of these are to uncover prey. Some appear to be exploratory, given here and there without digging into the wood, either to cause a wood-boring larva to move within its tunnel and thus reveal its location or to sound out difference in resonance between a hollow tunnel and solid wood.

Scaling.—When working on limbs that have been dead for some time, Crimson-crested Woodpeckers may combine pecking with sidewise, glancing blows that dislodge sizeable pieces of loose bark and other debris that may shower to the ground as the woodpecker moves along. On the other hand, almost nothing may fall when a woodpecker is working on the closely adherent bark of a dying limb; the powerful, rapid, occasionally prying blows involved in its straightforward pecking being sufficient to uncover prey.

Probing.—Putting the bill into natural cavities or clumps of epiphytes, etc., presumably to explore their interstices with their tongues, although these are seldom visible.

Digging.—When working on well rotted stubs for deeper lying prey, Crimson-crested Woodpeckers may dig cavities 10 cm or more deep, seizing and tossing larger slivers of rotten wood to the ground as they do so. The sizes of such cavities are usually no larger than those made by Hairy Woodpeckers (*Dendrocopos villosus*) and never as large as the deep troughs dug by Pileated Woodpeckers in North America. This doubtless reflects the fact that conditions of decay and location of insects are different in tropical climates.

The listing of these categories of feeding and foraging does not provide a full picture. As pointed out lucidly by Bock and Miller (1959) the *Campephilus* group of woodpeckers have remarkable adaptations not only in the forward direction of all their toes, but particularly in having legs directed away from the center of the body in such fashion that the full tarsus can be pressed against trunks and branches. The result is that such a species as *C. melanoleucos*, in whatever position it is working, whether on the underside of a limb, on the smooth bole of a large tree, or out on smaller branches, appears to be solidly stabilized for delivering powerful blows.

Feeding of non-breeding pairs in dry season.—Observations on a pair without attendant young, followed for 140 minutes on 24 February 1965 on Barro Colorado Island, brought out some aspects of feeding when the woods were relatively free of leaves. The two birds were usually within 15 m and often much less of each other as they moved through the mature forest feeding at heights varying from 6 to 25 m, the latter height bringing them close up under

the canopy of larger trees. Most of their feeding, however, was at intermediate levels. An almost constant feature with this pair was the greater activity of the female, for she was not only the first to fly on the six occasions when the woodpeckers flew from one part of the woods to another, but she also moved along a greater extent of limbs and tree trunks in feeding than the male. At one time, for example, both woodpeckers flew to a dead limb 4 m long. During the next 10 minutes she progressed nearly the whole length of the limb in knocking off bark and debris while he moved only a fifth as far as he probed thoroughly in a limited area, which he continued to do after she had left. His inclination to work one place thoroughly was again exemplified later in the morning. This time he was on a tree with a relatively smooth bole where he found large numbers of grubs under a strip of discolored bark and fed on them for 15 minutes. When any fell, he would press his belly against the bark to recover them.

Foraging in the rainy season.—The dry season arrived late in Panama in 1971 so that essentially all observations made from November into the latter part of January were made in the rainy season. They were divisible into two categories of which the first was in the second-growth woods at Cardenas Village. Here at 16:40 on 4 January, when Female A was presumably incubating, I found MA working alone on a small semi-dead tree, 3 to 4 m above the ground and at the level of my eye as I stood on a slope above. At times he moved out onto branches of 2.5 cm in diameter. Clinging securely by grasping small branchlets, two of his forward-directed toes on one side and two on the other, he pecked steadily on the still adherent bark, as if finding considerable amounts of prey. At one time, for example, I saw him extract a larva grub about 3 cm long. At another time he clung to the underside of a slightly larger branch, his forward directed toes serving well for hanging in this position. It is likely that insect larva are particularly abundant on the underside of limbs and branches where moisture collects and persists longer than on the uppersides. The male also worked on a limb of 10 cm in diameter. Here I could see that he delivered three or four powerful pecks in one place, then moved along to another, pecking rapidly and nowhere penetrating deeply into the wood. With a background of watching woodpeckers in the temperate zone, I would have thought the branches more suitable for a Hairy or even a Downy (*D. pubescens*) Woodpecker, than for a large species such as *C. melanoleucos*. Short (1970*a*) noted *C. magellanicus* feeding on small branches in a similar manner.

Crimson-crested Woodpeckers are versatile feeders whether in second-growth woods, such as those in Cardenas Village, or on Barro Colorado where the mature forest contained many large stubs and branches. Methods of feeding in these habitats are illustrated in the following examples. 1) Feeding

directly under bark. MA delivered hard blows on the firmly adherent bark of a dead stub near Cardenas Village and as bits of bark came loose, I could see tunnels of wood-boring larvae directly below. The woodpecker's blows were straight on, followed by a few at slight angles, together with prying motions. 2) Excavations into wood. A pair of Crimson-crested Woodpeckers on BCI dug holes 3 to 5 cm deep in a large stub finding not only small grubs, but also several large ones measuring approximately ½ by 4 cm. 3) Tree with smooth bark. A female fed under strips of loose bark on the unusually smooth bole of a large tree by splaying her legs well out to the side. 4) Possible feeding on termites. A lone female fed for 40 minutes on a dead stub arising from a small, understory tree. She dug so industriously into its basal portion that the upper part broke off and fell to the ground. Later examination of this portion revealed that it contained many termites along with a few tunnels, all old, of large larvae.

The foraging habits of Crimson-crested Woodpeckers were easy to observe for several reasons. First, the woodpeckers would often move from one tree to the next, finding plenty to look for without taking long flights from one good tree to another as is often the case with other woodpeckers, such as the Pileated or Hairy in northern woods; and second, when feeding high up on dead limbs, they would often move along the underside where one still had a good view of their activities.

COMPARATIVE FEEDING BEHAVIOR AND INTERACTIONS WITH *D. LINEATUS*

Crimson-crested and Lineated Woodpeckers fed in the same locations and occasionally on the same trees on Barro Colorado Island without signs of hostility or indeed special reactions of any kind.

I heard, for example, vocalizations of both species, then found the four woodpeckers of two pairs intermixed as they fed among a small group of trees on 24 December. When the Crimson-cresteds left, the Lineated Woodpeckers moved into the tree where they had been. Here the male probed into holes and crevices of a dead limb, then moved out onto a dead branch 2.4 cm in thickness that one would have thought suitable only for a smaller species. I had noticed a female Lineated Woodpecker doing much probing a short while before and an impression that this method of foraging was a characteristic habit of *D. lineatus*, more so than of *C. melanoleucos*, was re-enforced by further observations on 5 February. Thus, at 09:00 I heard both the *kwirr-as* of Crimson-crested and the *wer-wer-wer* notes of Lineated Woodpeckers coming from close by a trail. Sounds of digging then led me to a male Lineated. He pecked only briefly, then began probing a spot on the upper side of a large limb, 15 cm below a decaying branch stub. This was probably a ramifying area of decay, for the male turned and twisted his head for the next five minutes, as though reaching into deep tunnels or interstices with his tongue, the whole performance being identical with what I have witnessed with Pileated Woodpeckers on many occasions. It seemed probable, therefore, that the Lineated Woodpecker was foraging on ants and their larvae.

At 09:10 a male Crimson-crested suddenly alighted only a meter below the male

Lineated Woodpecker. As the Crimson-crested Woodpecker hitched upward, neither he nor the Lineated Woodpecker raised their crests in even mild excitement. When the two were within 30 cm, the Lineated flew to a limb a meter away, remaining there quietly while the slightly larger Crimson-crested Woodpecker took over his feeding place. The latter gave only a few pecks, as though finding nothing of interest, then moved on to drum once on the broken branch stub, preen briefly, and leave. The Lineated now returned to continue at his feeding spot for another 10 minutes.

A number of aspects of this episode were noteworthy. First, the Crimson-crested Woodpecker had not replaced the Lineated in a supplanting attack, for there was no sign of hostility, the situation appearing to be one of simple dominance at a food situation. The Crimson-crested was the larger woodpecker and this, plus having a longer, heavier bill, may have explained his dominance.

A second feature of the episode was that whereas the Lineated Woodpecker had started making *put-air* notes when I had arrived, he stopped making these notes when the larger woodpecker replaced him, appearing thus, if anything, to have become calmer, rather than more excited. What was the most significant feature of the encounter, however, was the light it threw on the feeding habits of the two species. The Lineated obviously found much to feed upon in the one spot, for he was able to feed there actively for a total of 15 minutes, quite possibly on ants and their larvae. On the other hand, the tree itself provided feeding places of a different kind, such as decaying dead limbs, attracting *C. melanoleucos*, for I had watched the male and female feeding here a few weeks before. These observations suggested the two species of woodpecker, instead of having the similar "ecologies" needed to support Cody's (1969) theory, can forage on the same trees for quite different sorts of prey. While they do undoubtedly overlap in some of their feeding habits, as indeed Tanner (1942) showed for Pileateds and Ivory-bills, this is not of sufficient degree to interfere with their being sympatric.

That the Lineated Woodpecker is specialized is seen most clearly, as is well discussed by Skutch (1969), in its attacks on *Cecropia*s and the colonies of *Azteca* ants harbored in their hollow trunks and branches. These trees grow in abundance nearly everywhere and their prevalence at edges of woods may explain why Lineated Woodpeckers come to these situations. On 9 January, for example, I found a male digging into a *Cecropia* at the edge of the laboratory clearing at Barro Colorado Island. He worked first on the trunk where it was 7 cm in diameter, then on a limb of half that thickness. Although I had many more observations on *C. melanoleucos* than on *D. lineatus*, I never saw it even alight on one of these fast growing trees which, in general, bear little dead wood.

I found it more difficult to observe the feeding habits of *D. lineatus* than those of *C. melanoleucos* for three reasons, namely that *D. lineatus* was more

easily disturbed, often starting *put-air notes* on seeing me; that it was more thinly distributed, being only one-third as numerous as *C. melanoleucos* on Barro Colorado Island; and finally that, whereas *C. melanoleucos* usually foraged from one tree to another close by, *D. lineatus*, after spending some time on one tree, might take a long flight to another and was hence easily lost to further observation. The last two situations suggested that *D. lineatus* requires larger feeding territories than *C. melanoleucos*. Whatever the differences between the two species, it was striking that they thrive together whether in old and mature woods such as at Madden Forest, Limbo, and Barro Colorado, or the second growth ones at Cardenas Village and Frijoles. It is of interest here, finally, that Slud (1964) found *D. lineatus* less common than *C. guatemalensis* in Costa Rica.

COMPARATIVE BREEDING BEHAVIOR OF LINEATED WOODPECKERS AND INTERACTIONS WITH *C. MELANOLEUCOS*

Skutch (1969) has provided a general account of the Lineated Woodpecker. Additional aspects based on recent observation are given below to bring out mainly how it is that *D. lineatus* and *C. melanoleucos* can live in sympatry without undue competition or overlap in any aspects of their lives. Reproductive isolation is, of course, complete. Not only are patterns of plumage colors about the head different, but also, and this may be of special importance, *C. melanoleucos* has a bright yellow iris while the iris of *D. lineatus* is strikingly white. This situation is depicted in color for *D. lineatus* and *C. guatemalensis* by Sutton (1951). The latter woodpecker forms a superspecies with *C. melanoleucos* and is also similar in plumage to *D. lineatus* with which it is sympatric. Short (1970*b*) noted that the eyes of an immature female of *C. melanoleucos* were white.

The drummings and vocalizations of *C. melanoleucos* and *D. lineatus* are also different. Thus, in *C. melanoleucos* the main call is a *kwirr-a* while in *D. lineatus* it is, according to Skutch (1969), a flicker-like *wic wic wic*. I have found, however, that this latter is actually part of a spectrum, becoming at high intensity a *wuk wuk wuk* of about 17 notes, falling off at the end, that one recognizes at once as being similar to the high call of the Pileated Woodpecker (Kilham, 1959), while at low intensities the notes become a *wer wer wer* that one might never consider as coming from a woodpecker. The drummings differ to an equal degree. Thus, much of the communication between members of a pair as well as between rivals in *C. melanoleucos* is by their peculiar drumming, vocalizations being infrequent. Comparable communications of *D. lineatus*, on the other hand, are more by vocalizations, while the long rolling drum, again like that of *D. pileatus*, is used less frequently.

Nest excavation.—Crimson-crested and Lineated Woodpeckers are further

TABLE 1

SIMPLIFIED OUTLINE OF DIFFERENCES IN BREEDING AND OTHER HABITS OF CRIMSON-CRESTED AND LINEATED WOODPECKERS THAT PERMIT SYMPATRY WITHOUT UNDUE COMPETITION*

Differences	*C. melanoleucos*	*D. lineatus*
Main breeding season	Last of rainy season and first of dry season (Nov.–Jan.)	Last of dry season (March–April)
Relative size of territories	Small	Large
Type of stub used for nesting (optimal)	Large (45–50 cm diam.); substantial	Stubs or tops of stubs small in diam. (18–23 cm); more risk
Food	**Larvae of wood-boring beetles primarily and possibly termites	*Azteca* and other ant larvae, overlaps with *C. melanoleucos* otherwise in feeding on beetle larvae
Temperament	Relatively tame	Easily alarmed

* It should be emphasized that this outline is based on observations of relatively few individuals.
** Special adaptations of feet and legs (Bock and Miller, 1959) make *C. melanoleucos* especially efficient at extracting this type of prey. (See text.)

isolated reproductively by the timing of their nestings, that of *C. melanoleucos* coming at the end of the rainy season and that of *D. lineatus* toward the end of the dry season (Table 1). W. John Smith (pers. comm.), for example, found a pair of *P. melanoleucos* nesting at Frijoles on 27 January 1967 not far from where a pair of *D. lineatus* had nested in May 1966, and Chapman (1929) mentions the young of a pair of *C. melanoleucos* as leaving their nest on Barro Colorado in February. Skutch (1969) stresses that the closely related *C. guatemalensis*, which replaces *C. melanoleucos* northward of Panama and is also sympatric with *D. lineatus*, is an unusually early nester. Although Lineated Woodpeckers nest later than Crimson-crested, they may, in some cases, start trial nest excavations early in January, as indicated by the following observations: On 2 January I found a pair of Lineated Woodpeckers excavating a hole in the dead top (Fig. 4) of a living tree, one of the Bombacaceae. The cavity was already deep but the two birds continued to toss out sawdust from the entrance until 4 January, when the excavation appeared to have been completed. Yet with exception of a brief view on 5 January I never saw the pair by the hole again. Strong winds came with the beginning of the dry season later in the month and on 1 February I found that the top of the tree had broken off where the cavity of the woodpeckers had weakened it (Fig. 4).

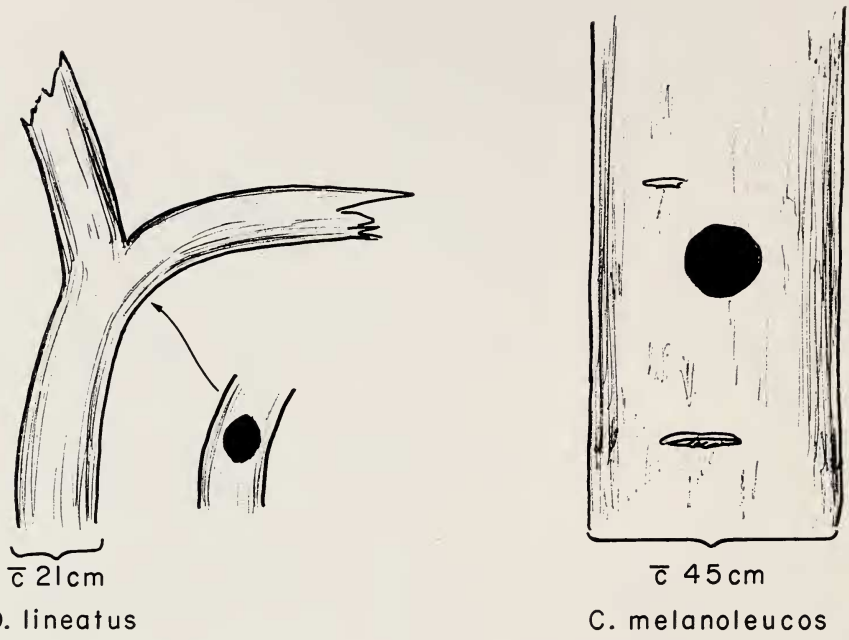

Fig. 4. Contrasting sites of nest excavations of Lineated and Crimson-crested Woodpeckers. (The entrance hole of the Lineated's nest having been under the curving arch of the limb above, is shown as seen from below, looking up.)

On 8 January on BCI a pair of Lineated Woodpeckers were excavating a hole they had pirated from a pair of the smaller Black-cheeked Woodpeckers (*Melanerpes pucherani*). The hole was in an arching limb 18 cm in diameter at the top of a tall dead stub. Both members of the pair of larger woodpeckers could enter their excavation completely by 9 January. The male was still excavating a week later but on 17 January the entire stub crashed to the ground.

In summary of these and other observations it would seem that *D. lineatus* differs from *C. melanoleucos* in the locations as well as in the timings of its nest excavations. Thus, while *C. melanoleucos* is particular about finding a large stub (Fig. 1) that will be a secure place to nest and appears wary about even attempting to nest otherwise, *D. lineatus* is attracted to inherently more risky situations, whether in stubs or in dead tops of trees so narrow that the nest cavity is barely accommodated. Its walls, therefore, are necessarily thin, offering too little support in case of wind or storm. Advantages of using such situations, however, must outweigh disadvantages. They may include such things as freedom from competition with the sympatric *C. melanoleucos* for

nest stubs, locations so high above ground as to be less within reach of usual climbing predators, and in being less attractive in their fragile nature to nest hole competitors of various species such as Collared Araçari.

Finally it should be noted that this habit of making nest excavation in places that would seem too narrow and too risky is not confined to *D. lineatus*. As previously described (Kilham, 1959) the same situation holds for Pileated Woodpeckers in central Florida where, in absence of any large trees, they may nest in narrow pole-like dead pines where a full nest cavity may be supported by little more than outer bark. Truslow (1967), who happened to be present at the dramatic moment, has recently photographed the breaking up of one such nest under only a light wind.

DISCUSSION

The Crimson-crested and Lineated Woodpeckers, whose breeding and feeding habits have now been compared, are a remarkable pair of species in being alike in size and general coloration, yet sympatric within the same monsoon-rain forest habitat. Thanks to Cody's article (1969), I became interested in studying these species concomitantly. If it were true, as Cody claimed, that these two are so alike in habits that they can coexist sympatrically only by means of an interspecific territoriality promoted by convergence in size and plumage patterns, then here was a remarkable biologic phenomenon. Unfortunately, I could find no evidence supporting Cody's ideas, for I was struck, as also was Karr (1971), that the two species are mutually tolerant. Every time I encountered Lineated Woodpeckers on Barro Colorado Island, for example, they were within the territories of one or another of pairs of Crimson-crested Woodpeckers under study. At no time did I observe conflicts such as might arise from mutually exclusive territoriality. The general peacefulness between the two species was notable not only when pairs happened to be feeding on adjacent trees, but also on one occasion when a male Crimson-crested, coming close to a male Lineated Woodpecker, temporarily displaced it from a feeding spot without show of hostility on the part of either the dominant or of the submissive species.

Having concluded early that interspecific territoriality did not exist, I wondered whether Cody's theory might not be modified to apply to spacing out in relation to nest sites. This hypothesis, however, likewise became untenable in the light of experience. The two species are divergent in such important aspects of their lives as the time of their breeding, the nature of nesting sites they look for, as well as in their feeding habits, as summarized in Table 1. Such a situation is, of course, the usual outcome of natural selection. What is unusual, if not very rare, would seem to be interspecific territoriality based on any long term evolutionary process.

An interesting example of limited interspecific territoriality among very closely related woodpeckers is given by Selander and Giller (1959). They found that, seemingly due to man's interference with natural ecologic barriers, morphologically similar members of the same superspecies, *Centurus carolinus* and *C. aurifrons*, met in Austin, Texas, and, in a limited area of sympatry, held mutually exclusive territories. This situation would appear different from what must be the historically long sympatry that has existed between *C. melanoleucos* and *D. lineatus*.

From one point of view an instructive example of a species pair comparable in some ways to the Crimson-crested and Lineated Woodpeckers, and even more alike in plumage although dissimilar in size, are the Hairy and Downy Woodpeckers. I have found (Kilham, MS) that in spite of wide differences in prey and feeding habits, in type of nesting sites, as well as in the time of onsets of breeding behavior, these species must still be acted upon by many selection pressures in common, such as predation, survival over winter months when trees are bare of leaves, and many others, in relation to which their plumages represent one of many optimal compromises for survival. While the selection pressure may differ from tropical rain forest to north temperate woodlands, the principles of why certain birds are similar in plumage would seem to be the same.

SUMMARY AND CONCLUSIONS

Reproductive and feeding habits of Crimson-crested Woodpeckers were followed in mature as well as in second-growth woods of the Panama Canal Zone.

The double drum *DA-drrr*, characteristic of *Campephilus* woodpeckers, was a main method of communication, whether used to express mild alarm, territorial dominance, or in duets between members of a pair at time of courtship.

Copulations and excavations were seen in November but most pairs had difficulty finding suitable nest stubs and either began nesting in December or January or, in some cases, failed to nest.

Territorial conflicts between rival males were marked in January, the intrusions being largely by males of pairs that were failing to establish nest holes.

Both sexes excavate and the bird excavating drum-taps on the inside or outside of the cavity on the arrival of its mate. This drum-tapping ceremony is identical in *Campephilus* and *Dryocopus*.

Bill-touching or fencing between members of a pair takes place at the nest excavation or elsewhere at the height of courtship.

Crimson-crested Woodpeckers become silent and difficult to observe in the incubation period, sitting on their eggs for prolonged periods without looking out from nest holes.

After hatching, either sex may look out and in the first few days when brooding young, drum-tap on the arrival of a mate. Prey was never visible in the bills of parents coming to feed young in the first three weeks.

A bird in adult female plumage, seeming by her begging behavior to be a young one of the year before, was seen accompanying a pair of Crimson-crested Woodpeckers in January. The male fed her a large grub on one occasion. Juveniles of recent nestings were first seen late in January and in February.

Crimson-crested Woodpeckers have remarkable adaptations of legs and toes which enable them to cling securely when feeding in such difficult situations as the undersides of limbs, small branches, or on boles of large trees. Larvae of wood-boring insects appear to be their chief prey.

Crimson-crested Woodpeckers live in the same woods and even feed in the same trees with Lineated Woodpeckers, which appear remarkably like them in size and general coloration. The two species differ in feeding habits, in time of onset of nesting, and in types of nest sites chosen. No signs of interspecific hostility or territoriality were observed.

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